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RESPONSES OF PLANT COMMUNITIES IN WESTERN FLORIDA BAY TO THE DIE-OFF OF SEAGRASSES

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ABSTRACT

Seagrass habitats in western Florida Bay have been undergoing changes from monotypic *Thalassia testudinum* meadows to large landscapes of barren bottoms or to increasingly heterogeneous *Thalassia* meadows as a result of seagrass die-off patch formation. The cause of this die-off is unknown but current hypotheses point to environmental stress making this seagrass susceptible to disease. The potential exists for colonization and recovery of these die-off patches but the sequence of events and the persistence of the recovery have not been evaluated. Based on an existing model that represents theoretical successional steps toward the *Thalassia* climax, four habitat types were sampled in each of two basins of western Florida Bay. Data demonstrated a high potential for recovery of the denuded die-off patches. The alga *Batophora oerstedii* is the first colonizer with replacement by other algal species and subsequently *Halodule wrightii* and eventually *Thalassia*. Under the existing conditions of high resuspended carbonate sediment and biological turbidity, which are thought to be secondary responses of the system to the die-off of seagrasses, persistence of the colonizing habitats and the climax community itself is tenuous. Decreases in both *Halodule* and *Thalassia* in non-die-off areas of Johnson Key Basin between spring and fall 1991 occurred as did decreases in densities of these species in recovering patches. Subsequent visits in 1993 revealed that the sample sites were devoid of seagrasses.

Florida Bay is a relatively shallow lagoonal system at the southern extreme of the Florida peninsula. This system is a complex of seagrass-dominated subtidal environments interrupted by numerous carbonate mud banks and mangrove islands (Thayer and Chester, 1989; Zieman et al., 1989). These habitats sustain important recreational and commercial fisheries both within and outside of Florida Bay (Powell et al., 1989; Thayer and Chester, 1989; Tilmant, 1989; Chester and Thayer, 1990).

In the mid-1980's seagrasses covered more than 80% of the 1,800 km² area of Florida Bay within the boundaries of Everglades National Park (Zieman et al., 1989; Robblee et al., 1991). Changes have occurred in these seagrass habitats during the last three decades that appear to have influenced fisheries. During the late 1960's and 1970's there was a transition from heterogeneous seagrass meadows with mixtures of pure stands of *Halodule wrightii* and *Thalassia testudinum* toward communities dominated by *T. testudinum*, the climax community for the system. This is hypothesized to be the result of a combination of both natural and human activities with long-term decreases in freshwater inflow and decreased frequency of hurricane-induced destabilization of the system being considered most important (Zieman et al., 1989). Coincident with this succession to a more monospecific seagrass habitat has been an overall decline in recreational gamefish populations (Tilmant, 1989).

In summer 1987 a different expression of environmental changes in Florida Bay was observed, with numerous and extensive bare patches occurring in many of the dense *Thalassia* meadows, particularly those in western Florida Bay (Robblee et al., 1991). The "die-off" patches may coalesce to form expansive bare areas within an otherwise homogeneous meadow, thereby forming a heterogeneous environment; in some instances entire basin areas may become totally devoid of seagrass. These die-off events continue to occur in the western region of

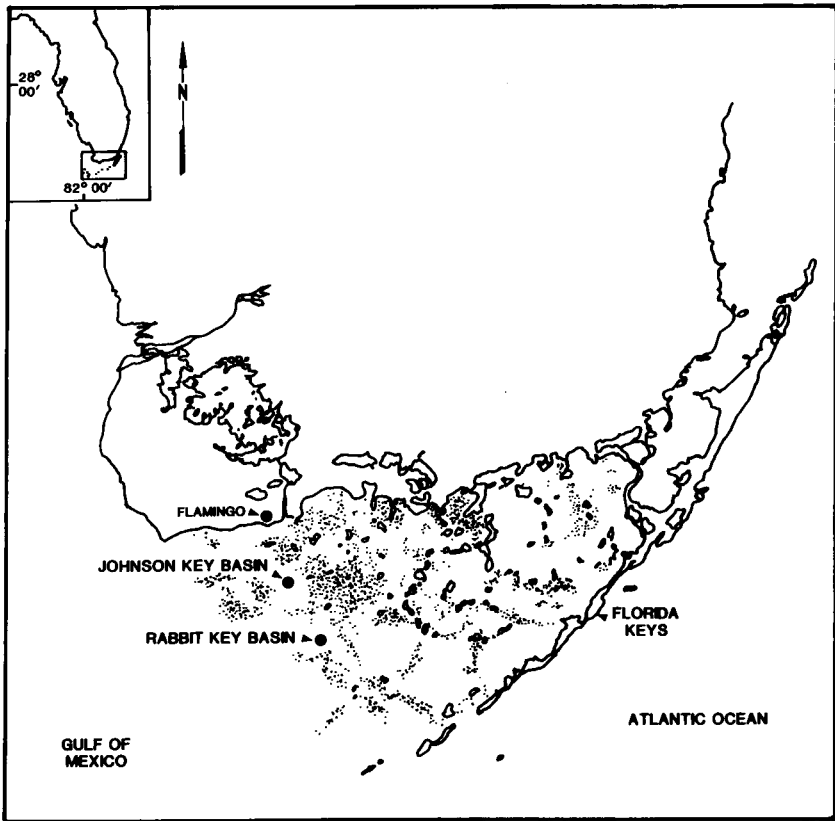


Figure 1. Diagram of Florida Bay showing the general location of Johnson Key Basin and Rabbit Key Basin.

Florida Bay that has displayed the most dense and diverse fishery communities (Thayer and Chester, 1989; Chester and Thayer, 1990; Robblee et al., 1991) and, consequently, may result in modification of fishery resources and/or fishery-habitat interactions. Durako et al. (in press) have summarized the current hypotheses on the die-off, and indicate that the most plausible hypothesis centers on weakening of *Thalassia* by environmental stresses making it vulnerable to disease.

The die-off areas may not remain devoid of vegetation but can become colonized, thereby increasing plant heterogeneity within many sections of the bay. Although Robblee et al. (1991) suggest that *H. wrightii* may show a rapid increase in density in some of the patches, there are no published data available to indicate how widespread or persistent the recovery is, nor has there been an evaluation of the sequence of succession in these disturbed Florida Bay habitats. In this paper we concentrate on the changes that occur within different seagrass patch types in two basins of western Florida Bay.

MATERIALS AND METHODS

Sampling Location.—Study sites were located in western Florida Bay in Johnson Key Basin and Rabbit Key Basin (Fig. 1). Johnson Key Basin (JKB) sites were established along the edge of Sandy Key Bank in water depths of 0.7–1.5 m. Sampling was conducted at approximately 6-week intervals

between July–October 1990 and again from April 1990–November 1991. Sites were established in the southeastern portion of Rabbit Key Basin (RKB) adjacent to Ninemile Bank in water depths of 1.2–1.6 m; sampling was conducted here for only the period June 1991–November 1991. In both instances, sampling was terminated in November 1991 due to excessive turbidities which resulted in our inability to evaluate the sites effectively. The sites were selected in four habitat types based on the model for developmental patterns of seagrass communities in south Florida presented by Zieman (1982). In this model, under stable environmental conditions sandy/muddy substrates can be colonized initially by macroalgae and subsequently by *H. wrightii* followed by *T. testudinum*. Thus, we selected four habitat types: (1) dead areas that had recently been occupied by living *Thalassia* as indicated by the presence of dead leaf and rhizome material; (2) algae dominated patches; (3) patches dominated by *Halodule*; and (4) areas of undisturbed *Thalassia* meadow. In all but the latter, evidence of dead *Thalassia* rhizomes still existed.

Six representatives of each habitat type were visually selected over approximately a 1 km distance in each basin. In each case, selected patches were at least 3×3 m in dimension and about 3–5 m from any adjacent sample site. Once selected, a site was marked and sampled on successive sampling dates.

Sample Collection, Processing and Analysis.—Plant coverage and density were sampled using a modification of Fonseca et al. (1990), in which a 1-m² quadrat subdivided into 16, 0.062-m² subsections was placed in the center of each sample site. Plant cover was estimated by recording the number of subsections with at least one seagrass short shoot or alga. Seagrass short shoot and individual algal plant densities were estimated by counting the number of shoots or individual species/genera of algae in three randomly selected vegetated subsections. When there were in excess of 40 shoots/subsection, a 0.01-m² quadrat was placed in the center of the subsections and density counts made. Short shoot and algal densities were computed as areal density by multiplying the m² density by the percent bottom covered within a quadrat. Short shoot and algal densities were log-transformed (+1) and analyzed using 1-way ANOVA by sampling month. When F-tests indicated significance Duncan's Multiple Range Test for comparison of means was employed.

RESULTS AND DISCUSSION

Our selection and assessment of four habitat types within the two basins was predicated on a temporal successional sequence including undisturbed *Thalassia* distant from existing die-off areas, die-off patches colonized by algae and subsequently *Halodule* and eventually *Thalassia* (Zieman, 1982). By selecting these habitats as an indication of successional development as opposed to following a series of bare die-off patches over time, we hoped to obtain a picture of the sequence of succession compressed in time, recognizing that the age of any one of the patches would not be known.

Undisturbed *Thalassia* habitats.—The undisturbed seagrass community in both JKB and RKB was dominated by *Thalassia*, with the major difference between basins being the presence of a substantial understory of *Halodule* (389 short shoots·m⁻²; July 1990) in JKB (Fig. 2). In RKB *Thalassia* interseasonal short shoot densities were fairly stable between June and November 1991 with mean densities ranging from 960–1,333 short shoots·m⁻²; *Halodule* only appeared in the samples during September at a mean density of less than 6 short shoots·m⁻².

A decrease in abundance of *Halodule* between spring 1991 and fall 1991/summer 1992 (weakly significant at $P = 0.10$), and that of *Thalassia* in both JKB and RKB during the same period (both significant at $P < 0.05$) was observed and may be the result of increased light attenuation within the basins of western Florida Bay. Further, the decrease in *Halodule* density from a mean of 259 shoots·m⁻² in 1990 to less than 20·m⁻² in November 1991 and non-existent in August 1992 suggests a synergistic effect between increased light attenuation from turbidity coupled with existing attenuation within the *Thalassia* canopy. This occurred even though densities of *Thalassia* were decreasing. With the increase in area of seagrass die-off, biogenic and anthropogenic turbidity in western Florida Bay has increased considerably (Durako et al., in press; R. D. Jones and J. B. C.

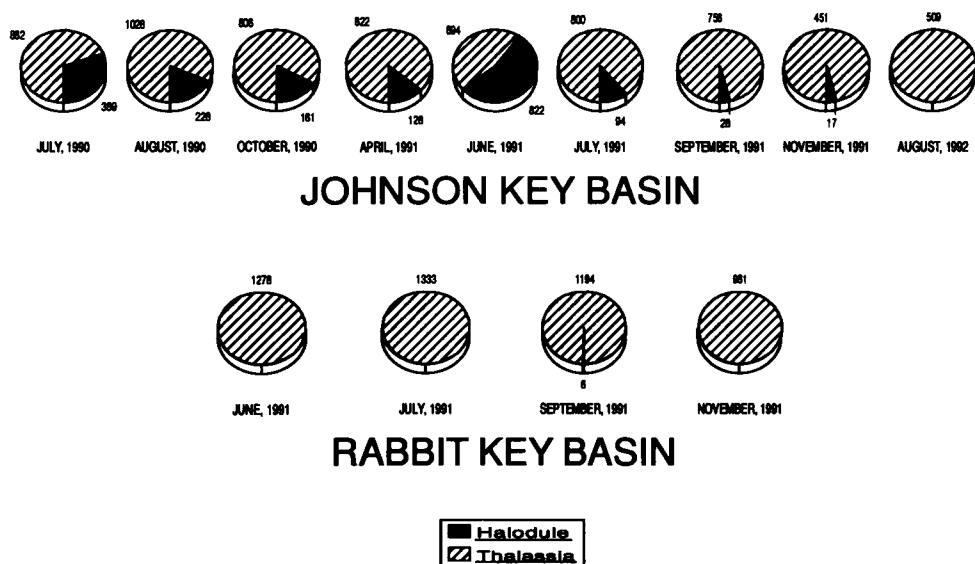


Figure 2. Mean abundance of seagrasses in Johnson Key Basin and Rabbit Key Basin in short shoots m^{-2} based on six samples on each occasion (see text for details).

Bugden, Florida International Univ., pers. comm.; M. B. Robblee, Everglades National Park, pers. comm.; M. J. Durako, Fl. Mar. Res. Inst., pers. comm.; pers. obs).

Jones and Bugden (Florida International Univ., unpubl.) currently are collecting water quality data in Florida Bay which includes turbidity values in nephelometer turbidity units (NTU). Their data show mean NTU values increasing from 2.80 in May 1991 to in excess of 5.00 in September–October 1991 and 8.69 in December 1991 for 10 stations throughout the southwestern and western portion of the Bay. Values for two stations in Johnson and Rabbit Key Basins increased from about 0.2 to 0.7–0.9 NTU between March and December 1991, and to 3.0–9.9 NTU between March and May 1992. Based on work by Alleman (1991) in Biscayne Bay, the NTU values recorded for JKB and RKB are suggestive of light attenuation coefficients indicative of light limitation to seagrasses, even at water depths of about a meter.

Our suggestion of probable light limitation is supported by experimental evidence from shading and physiological studies and research on transplanting of these two species. Hall et al. (1991; unpubl. data) conducted a series of shading studies in which *Thalassia* short shoots were reduced 25–60% over a 13-month period; the slowness of this response was attributed to below-ground storage reserves. Fonseca and Kenworthy (NMFS, Beaufort Laboratory, unpubl.) have conducted transplanting experiments that demonstrate a high mortality rate for *Halodule*, and hypothesize that this species is more prone to mortality induced by sustained perturbations to water transparency than is *Thalassia* (Fonseca and Kenworthy, pers. comm.). Based on the fact that *Halodule* only has limited storage reserves to draw on during periods of low light availability, they hypothesize that long-term reduction in light will slow asexual reproduction and lower the plant's ability to compensate for the high mortality observed.

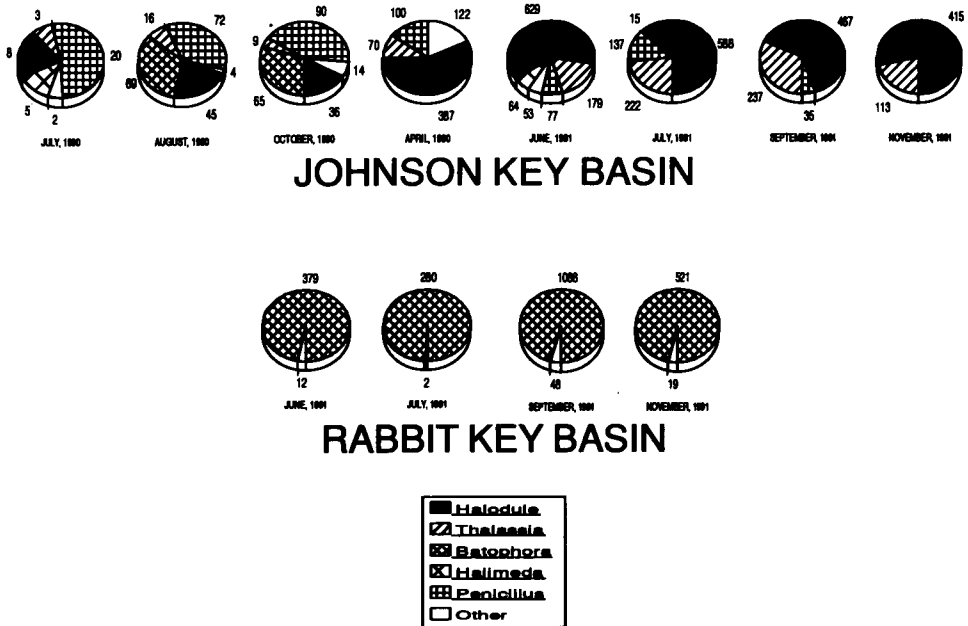


Figure 3. Mean abundance of algae (individual plants) and seagrasses (short shoots)-m⁻² at seagrass die-off sites initially classified as “dead” or early die-off sites in Johnson Key Basin and Rabbit Key Basin.

Dead and Algal-dominated Habitats.—The patches categorized initially as “dead” in fact were not devoid of vegetation but appeared to be in an earlier successional stage than those classified as algal-dominated sites. Initially, dead sites in JKB were comprised of a diverse plant community consisting of *Penicillus* spp., *Halimeda* spp., *Batophora oerstedii*, *Thalassia*, and *Halodule*, all at low densities (Fig. 3). The six sites selected in RKB were dominated by a single species of alga, *B. oerstedii* (Fig. 3). There was a rapid increase in density of this alga during summer followed by a decrease by late fall. This supports Morrison’s (1984) observations at Key Largo that *Batophora* is a summer-adapted plant.

There was a significant difference ($P < 0.001$) in the density of total algae in JKB over time, with total densities being significantly lower during July 1990, 1991, September and November 1991 than at other times. After exhibiting low densities at the start of our sampling of this habitat type *Halodule* and *Thalassia* represented the majority of the plant community standing stock and displayed mean densities of about 600 and 200 shoots-m⁻², respectively, 12 months later (Fig. 3); the increase in density of *Thalassia* from 1990 to 1991 was significant at $P < 0.01$ whereas that for *Halodule* was not. However, as occurred in the non-die-off *Thalassia* sites, densities of both species decreased during 1991.

While the age of the successional stage habitats originally selected was not known, we did establish that *B. oerstedii* is the first colonizer of barren die-off patches in both western Florida Bay basins, and conclude that the “dead” and algal-dominated patches sampled in RKB (Fig. 3) were more recent victims of the die-off than those in JKB (Fig. 3). Numerous recent die-off patches appeared in our sampling universe during sampling, and four were marked and followed (Fig. 4). By June 1991 these patches had a mean standing stock of *Batophora* of

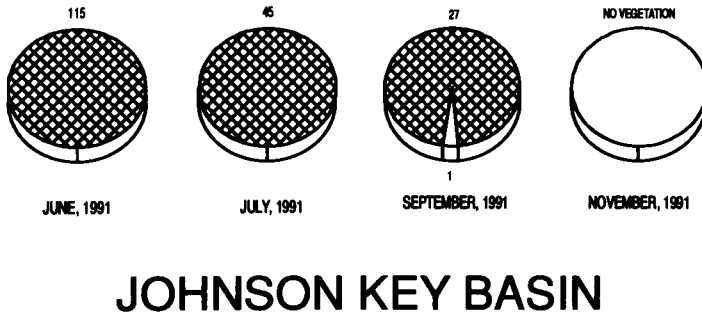


Figure 4. Mean abundance of *Batophora oerstedii*-m⁻² at sites in Johnson Key Basin that had been dense *Thalassia testudinum* in April 1991 but which had experienced a recent seagrass die-off event.

115 plants-m⁻². This was a transient stage, however, and the patches were devoid of vegetation the following November. The dramatic decrease observed probably is a response to increased light attenuation since Morrison (1984) showed this to be a summer-adapted plant with maximum densities in summer and fall.

The habitat types initially classified as algal-dominated had a much more dense

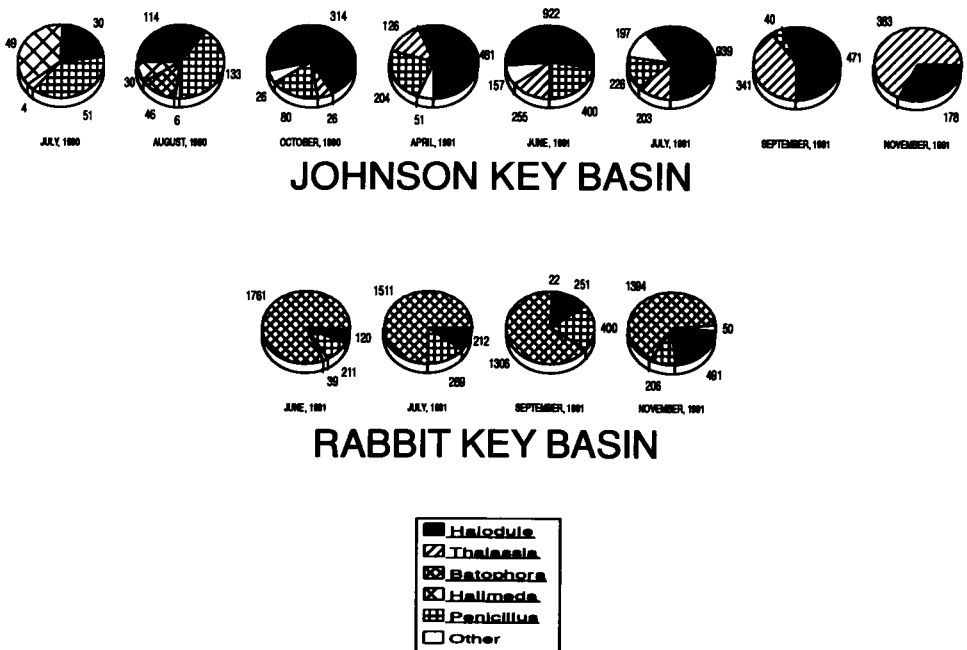


Figure 5. Mean abundance of algae (individual plants) and seagrasses (short shoots)-m⁻² in Johnson Key Basin and Rabbit Key Basin at seagrass die-off sites initially classified as algal-dominated.

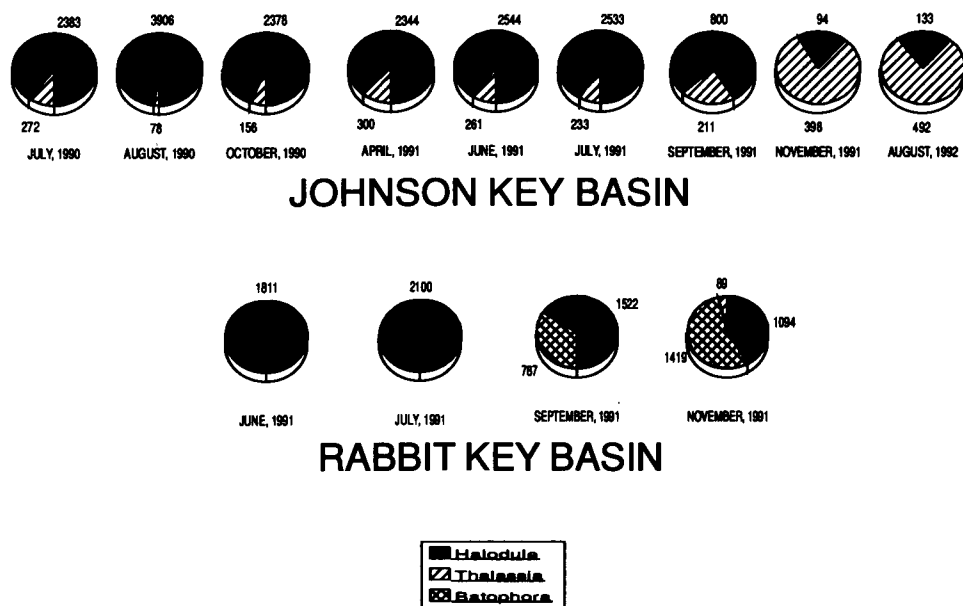


Figure 6. Mean abundance of seagrasses (short shoots) and algae (individual plants)·m⁻² at seagrass die-off sites originally classified as *Halodule wrightii*-dominated in Johnson Key Basin and Rabbit Key Basin.

plant community (Fig. 5) than those discussed above. With little exception, the community remained fairly stable in RKB, being dominated by *Batophora* and *Penicillus* spp. *Halodule*, which was present in June at a density of 120 short shoots·m⁻², increased in density by 4-fold by November while *Batophora* decreased from 1,761 to about 1,400 plants·m⁻². Both *Halodule* and *Thalassia* colonized these patches rapidly in JKB, increasing from respective means of about 30 and 4 short shoots·m⁻² in July 1990 to in excess of 900 and 200 short shoots·m⁻², respectively, 1 year later. By fall 1991, algae were no longer a component of the community, the decrease after June 1991 being significant ($P < 0.001$). As was noted for other habitat types within JKB, however, *Halodule* decreased dramatically in density between summer and fall 1991. Again we believe this is an apparent response to the increase in turbidity discussed previously.

***Halodule*-dominated Habitats.**—The final stage in the successional sequence leading to the climax *Thalassia* community proposed by Zieman (1982) is one dominated by *Halodule*. In the case of JKB, the succession appeared to be progressive whereas in RKB it appeared to be regressive (Fig. 6). In JKB the *Halodule*-dominated seagrass community was relatively stable between July 1990 and 1991 with a mean standing stock of 2,680 short shoots·m⁻² (range of mean values of 2,340–3,900) and a mean density of *Thalassia* short shoots of 217. *Halodule* densities decreased significantly ($P < 0.0001$) from July 1991 to November 1991 and August 1992 (Fig. 6). At the same time, *Thalassia* increased in standing crop density by 2-fold, and became the dominant seagrass canopy. These densities were equivalent to densities in the undisturbed *Thalassia* meadows nearby (Fig. 2) that appeared to be displaying light limitation stress. We speculate that colonization might have been more extensive had turbidity levels not increased.

At RKB, however, *Halodule* decreased in short shoot density by almost half during the sampling period and was replaced by *Batophora* beginning in September. This alga doubled its density between September and November 1991 at which time evidence of *Thalassia* encroachment was observed.

The rate of colonization of the *Halodule*-dominated patches by *Thalassia* at JKB was unanticipated based on available data on growth and transplant colonization rates (Zieman, 1982; Fonseca et al., 1987), particularly under the increased turbidities that western Florida Bay has been experiencing. Fonseca et al. (1987) showed that planting *Thalassia* on 1-m centers would result in a short shoot density of 300-m⁻² in 4.0–4.7 years. Durako (in press) reports, however, that small short shoots are characteristic of the Florida Bay die-off areas and that rhizome branching was initiated for every four short shoots. He observed that many of the short shoot meristems had branched to form twin short shoots originating from the same stem, frequently branching to form new rhizome apices. This unusual branching pattern could explain the observed rates of initial colonization of the patches by *Thalassia* from the surrounding seagrass meadow.

CONCLUSIONS

The data suggest that there has indeed been recovery of many of the unvegetated patches within *Thalassia* meadows within Johnson and Rabbit Key Basins. The die-off initially reported by Robblee et al. (1991), however, is still continuing. The sequence of stages in the succession from die-off patches to climax community appears to be initiated by the alga *B. oerstedii*, which is subsequently replaced by a number of other algal species and eventually the seagrasses *H. wrightii* and *T. testudinum*. This is in agreement with the model described by Zieman (1982). Based on our observations the potential for recolonization and recovery of these stressed habitats is high due to the relatively rapid growth rates of *Halodule* and possibly meristematic branching of *Thalassia* reported by Durako (in press). However, secondary effects of the die-off, which include increased bacterial densities, heterotrophic activity, dissolved organic carbon and nitrogen and the presence of algal blooms (Durako et al., in press), as well as increased resuspension of carbonate sediments, is resulting in increased turbidity and reduced light penetration. Our data indicate that these secondary conditions are exacerbating the impacts of the seagrass die-off in many parts of the Bay, and are resulting in reduction of the recovery process. In fact, subsequent visits to all sampling sites during summer–fall 1993 revealed that they were devoid of seagrasses.

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